

## Brief Communication: New Primate Remains From the Miocene of Namibia, Southern Africa

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**ABSTRACT** Miocene primates from southern Africa are extremely rare. For this reason we wish to place on record several interesting new fossil primate specimens recently recovered from the Miocene sites of Berg Aukas and Harasib in the Otavi Mountain region of northern Namibia. The new finds consist of a virtually complete atlas vertebra from Berg Aukas attributable to the hominoid *Otavipithecus namibiensis* and two teeth and four postcranial fragments from Harasib referable to Cercopithecoidea. The atlas vertebra exhibits anatomical characteristics intermediate between those of modern cercopithecoids and hominoids which may be indicative of a transition from pronograde to orthograde postures. The cercopithecoid remains show that the earliest Old World monkeys known from southern Africa were small, approximately the size of vervet monkeys. These new specimens are important because they provide the first evidence relating to possible positional behaviors of *Otavipithecus* and the earliest fossil record of cercopithecoids from southern Africa. © 1996 Wiley-Liss, Inc.

Evidence for the evolutionary history of Miocene primates in southern Africa is known from only two localities, both located within the Otavi Mountains of northern Namibia: (1) Berg Aukas, a series of Miocene–Holocene fossiliferous breccias that has yielded the late middle Miocene hominoid *Otavipithecus namibiensis*, and (2) Harasib 3a, a series of late Miocene breccias preserving a diverse array of fossil mammals including remains of Lorisidae (Conroy et al., 1992a,b, 1993a,b; Conroy, 1994; Senut et al., 1992; Pickford et al., 1994). Here we announce the discovery of several additional primate fossil specimens recently discovered from this region, including an atlas vertebra from Berg Aukas attributable to the hominoid *Otavipithecus namibiensis* together

with two teeth and four postcranial fragments from Harasib referable to Cercopithecoidea. These new specimens are important because they provide the first clues concerning the positional behavior of *Otavipithecus* as well as the earliest fossil record of cercopithecoids from southern Africa.

### ATLAS VERTEBRA OF *OTAVIPITHECUS NAMIBIENSIS*

We have recently recovered an atlas vertebra of a large-bodied primate from bone-bearing breccia block #BA 91-104 from the

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Table 1. Fauna found in the same breccia block with the atlas vertebra here assigned to *Otavipithecus namibiensis*<sup>1</sup>

|               |  |
|---------------|--|
| Insectivora   | Tenrecoidea indet.   |
| Macroscelidea | Macroscelididae indet.   |
| Chiroptera    | <i>Taphozous incognita</i><br><i>Tadarida</i> sp.<br>Molossidae indet.<br><i>Hipposideros</i> small sp.<br><i>Hipposideros</i> medium sp.  |
| Rodentia      | <i>Apodecter</i> sp.<br><i>Vulcanisciurus</i> sp.<br>Sciuridae large sp.<br><i>Notocricetodon</i> sp.<br><i>Protarsomys</i> sp.<br><i>Dakkamyoidea</i> sp.<br><i>Myocricetodon</i> sp. |

<sup>1</sup> *Vulcanisciurus* and *Notocricetodon* can be found in the Early Miocene, but by themselves are not sufficient to estimate the age of this block. However, the presence of *Vulcanisciurus*, *Notocricetodon*, and *Myocricetodon* in combination with the absence of such early Miocene forms as *Diamantomys*, *Bathyergoides*, a large *Paraphimys*, or *Afrocricetodon* are strongly suggestive of a Late Middle Miocene age.

locality of Berg Aukas, northern Namibia. As such, it is the only complete atlas vertebra known of an African Miocene hominoid. Other fauna recovered from the same breccia block suggest a late Middle Miocene age (~12–13 Ma) for the primate vertebra, an age similar to that determined for the type specimen of *Otavipithecus namibiensis* from the same site (Table 1). We are confident in assigning this primate vertebra to *Otavipithecus namibiensis* because this species is the only large mammal presently known from the site (Conroy et al., 1992a,b, 1993a,b; Conroy, 1994; Senut et al., 1992; Pickford et al., 1994).

The atlas is virtually complete with only slight erosional damage to the tips of both transverse processes and the superior articular facets. In overall dimensions it approximates the size of the atlas vertebra of a female chacma baboon (*Papio ursinus*), reinforcing the inference from the dentition that adult *Otavipithecus* weighed approximately 15 kg (Figs. 1, 2).

While there is no doubt that *Otavipithecus* is cladistically a hominoid (Conroy, 1994), its atlas displays an interesting mosaic of features that appear intermediate between those typically seen in more quadrupedal cercopithecoids (e.g., *Papio*, *Colobus*) and those in more orthograde hominoids (e.g., *Pan*, *Homo*). Hominoid-like features of the atlas include the more horizontal orientation of the superior and inferior articular facets

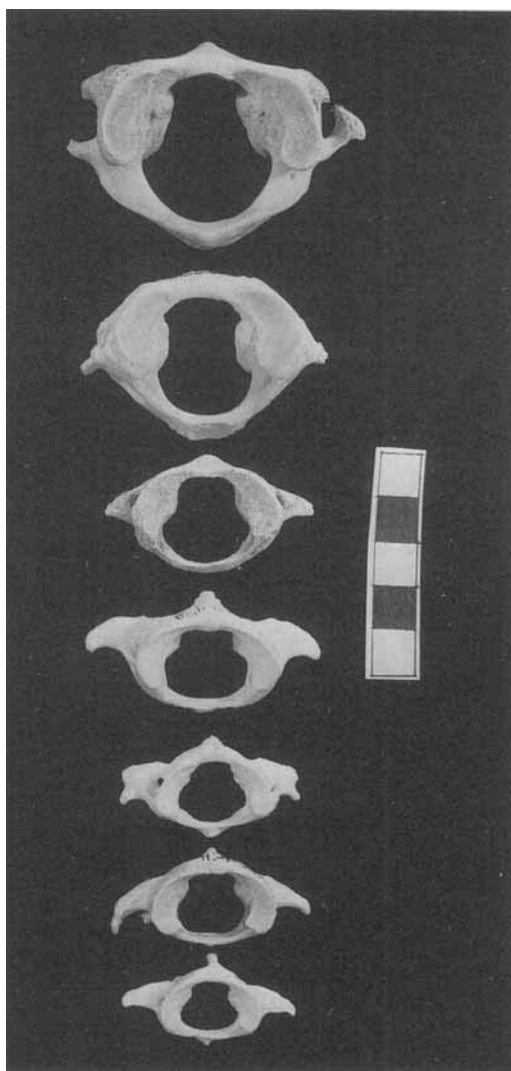


Fig. 1. Superior view of atlas vertebrae in several primates (from top to bottom): *Homo sapiens*, *Pan troglodytes*, *Otavipithecus namibiensis* (cast), *Papio ursinus*, *Colobus guereza*, *Mandrillus sphinx*, *Cercopithecus albogularis* (cm scale).

for articulation with the occipital condyles and axis vertebra, respectively (Fig. 3) and the overall reduction in the relative size and proportions of the transverse processes. This morphology contrasts with cercopithecoids who tend to have more vertically oriented superior and inferior articular facets (i.e., steeply sloped toward the vertebral canal) and transverse processes that are both rela-

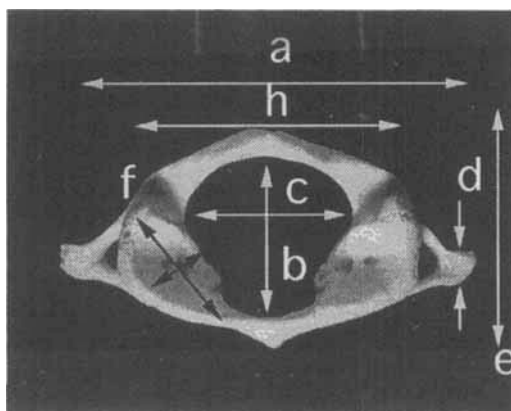


Fig. 2. Dimensions of the *Otavipithecus* atlas vertebra (in mm): **a**: maximum width, 46; **b**: maximum length of vertebral canal, 18; **c**: maximum width of vertebral canal, 18; **d**: maximum width of transverse process (lateral to vertebral foramen), 5; **e**: maximum (AP) length, 26; **f**: maximum length of superior articular facet, 16; **g**: maximum diameter of vertebral artery canal (not shown), 3; **h**: maximum breadth across superior articular facets, 33; **i**: lateral projection index of transverse processes ( $h/a$ ), 0.72; **j**: transverse processes width index ( $d/e$ ), 0.19; and **k**: overall shape index ( $a/e$ ), 1.77.

tively elongated (i.e., that extend well beyond the level of the transverse foramina) and wide at their base where they meet the vertebral arch. The more horizontally aligned superior and inferior articular facets in hominoids presumably reflect the greater surface area needed to balance the head in more orthograde postures. In these features the *Otavipithecus* atlas appears intermediate between the cercopithecoid and hominoid condition, i.e., the superior and inferior articular facets are less steeply inclined than in cercopithecoids but not so much as in hominoids, and the transverse processes do project laterally beyond the transverse foramina but are not particularly wide at their base where they meet the vertebral arch (Figs. 1, 3).

In the hominoid atlas the vertebral canal is greatly expanded dorsally relative to the position of the inferior articular facets. This dorsal expansion is not so prominent in cercopithecoids. Again, *Otavipithecus* appears intermediate in this feature. This dorsal expansion in hominoids provides more space for the important vertebral artery to enter the dorsal aspect of the foramen magnum

and, not unexpectedly, finds its greatest expansion in humans. It is probably for this reason that secondary vertebral foramina are much rarer in humans than in any other primate. As in many cercopithecoids and hominoids, the *Otavipithecus* atlas displays a bony bridge forming a secondary foramen through which the vertebral artery passes on its way to the foramen magnum.

In lateral view the superior face of the transverse process slopes markedly inferiorly in cercopithecoids but is more horizontally oriented in hominoids. Thus the anterior arch of the vertebral foramen is narrow in a superior–inferior direction in hominoids but wide in cercopithecoids. *Otavipithecus* is more hominoid-like in this feature. Cercopithecoid atlases also have more projecting, spine-like anterior tubercles, whereas these tubercles are blunter in hominoids and in *Otavipithecus*.

#### FIRST MIOCENE CERCOPITHECOIDS FROM SOUTHERN AFRICA

We have also recently recovered two cercopithecoid teeth from bone-bearing breccias at the nearby Miocene site of Harasib 3a, northern Namibia (Table 2; Fig. 4). These are the oldest cercopithecoid teeth yet discovered in southern Africa. Harasib is also the only site which documents the presence of Miocene prosimians in southern Africa (Conroy et al., 1993a,b). Prior to these discoveries at Harasib, fossil prosimians were unknown in southern Africa and the earliest cercopithecoids recorded from southern Africa were two isolated papionin premolars from the Pliocene site of Langebaanweg, South Africa (Grine and Hendey, 1981). Fauna associated with the Harasib cercopithecoids suggest a late Miocene age of ~9 Ma, i.e., equivalent to the European Upper Vallesian Land Mammal Age (Pickford et al., 1994).

While we hesitate to put taxonomic labels on such isolated teeth, one tooth, most probably a lower right  $dp_4$ , has a mosaic of features not expected in a single specimen (Fig. 4a). For example, the anterior fovea is long as in cercopithecines (and in *Victoriapithecus*; Benefit, 1994), but the lingual notch (taloid notch) is deep as in colobines. One other in-

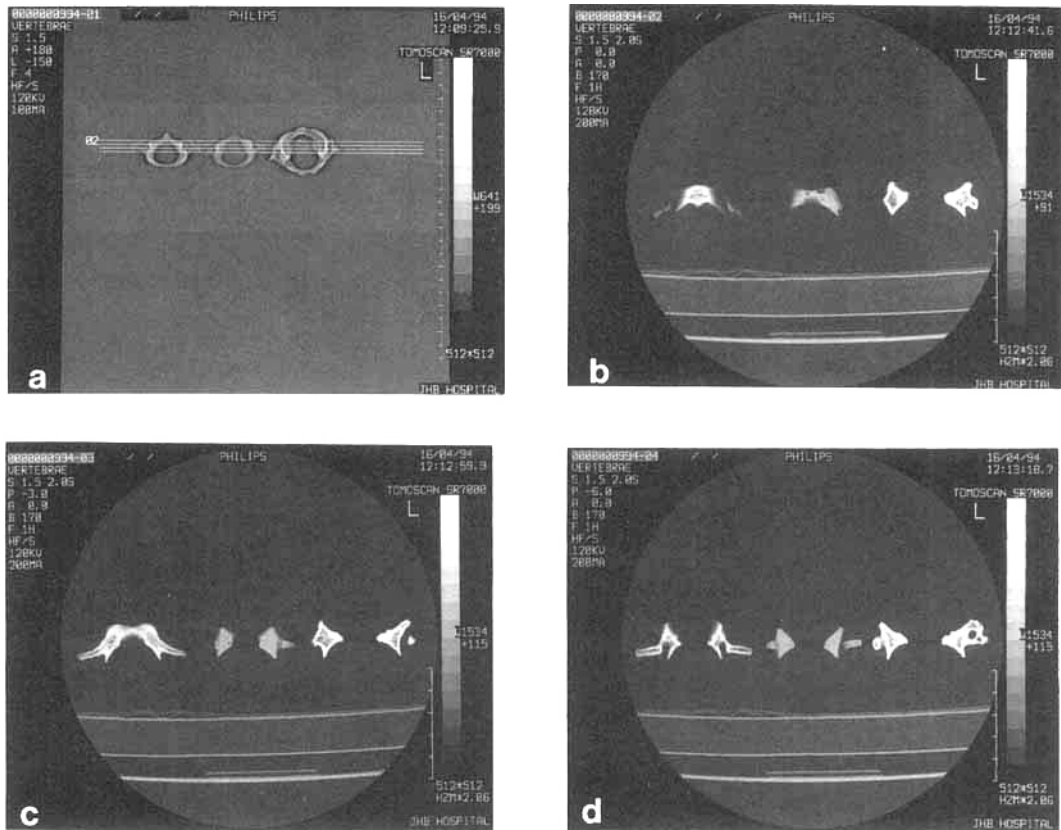


Fig. 3. Three contiguous coronal CT scans (1.5 mm) through the superior and inferior articular facets of atlas vertebrae in (left to right) *Papio ursinus*, *Otavipithecus namibiensis* (cast), and *Pan troglodytes*. Note the more steeply inclined plane of the superior and inferior articular facets in *Papio* as compared to *Pan*. *Otavipithecus* seems intermediate in this feature. **a:** Topogram showing orientation of CT slices. **b:** Slice 2. **c:** Slice 3. **d:** Slice 4.

TABLE 2. Dental dimensions (mm) of cercopithecoid teeth from Harasib (measurements defined as in Benefit, 1993)

|                                  | dp <sub>4</sub> | colobine M <sub>1</sub> or M <sub>2</sub> |
|----------------------------------|-----------------|---|
| Length (L)                       | 5.4             | 6.5                                       |
| Mesial width (MW)                | 4.0             | 5.1                                       |
| Distal width (DW)                | 4.4             | 5.1                                       |
| Mesial shelf length (MSL)        | 1.6             | 1.5                                       |
| Distal shelf length (DSL)        | 0.9             | 1.3                                       |
| Medial lingual notch height (NH) | 1.5             | 2.5                                       |
| Crown height (NR)                | 2.5             | 3.3                                       |

interesting aspect of this tooth is that the distal margin (marginal ridge along the back edge of the tooth) curves down from near the hypoconid apex and then up lingually but does not reach the entoconid apex, as it does in the more symmetrical configuration in

most modern cercopithecoid taxa (E. Delson, personal communication).

The second tooth, a lower right M<sub>1</sub> or M<sub>2</sub>, is clearly colobine in affinities (Fig. 4b). Several aspects of this tooth are reminiscent of features found in *Microcolobus* from the Miocene of Kenya (Benefit and Pickford, 1986). For example, both have moderately high cusps that are angled slightly mesially (*Nasalis*, *Pygathrix*, and *Rhinopithecus* display taller and more vertically oriented cusps) and the mesial and distal foveal lengths are approximately equal (distal shelves are longer than mesial shelves in such African fossil colobines as *Cercopithecoides*, *Rhinocolobus*, and *Paracolobus*) (Benefit and Pickford, 1986).

In addition to the two cercopithecoid teeth,

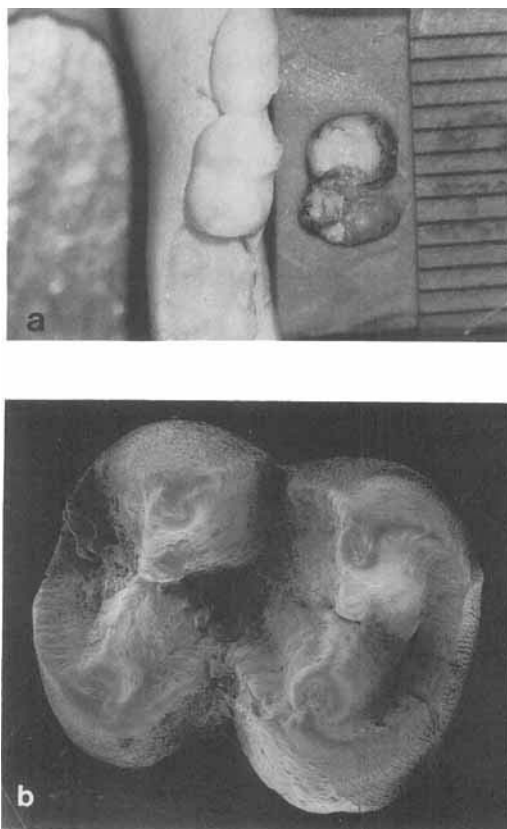


Fig. 4. **a:** Occlusal view of Harasib  $dp_4$  compared with a small *Cercopithecus*  $dp_4$  and  $M_1$  (mm scale). **b:** Occlusal view of Harasib colobine molar (tooth length = 6.5 mm).

four cercopithecoid postcranial fragments have also been recovered from Harasib 3a: a fragment of proximal right ulna, distal end of a metacarpal; distal end of a proximal phalanx (manus?); and distal phalanx (pedal?). Even though the fossils are for the most part fragmentary, they reveal that this species was of small size, about the size of the vervet monkey (*Cercopithecus aethiops*).

As the oldest cercopithecoids yet discovered in southern Africa, these fossils are of particular biogeographic significance. For example, the subfamily Colobinae is totally absent from the southern African region today and the subfamily Cercopithecinae is represented by only three species, *Cercopithecus aethiops* (vervet monkey), *C. mitis* (samango monkey), and *Papio ursinus* (chacma baboon). *C. aethiops* and *P. ursinus* are the only cercopithecines found today in

Namibia and their present distributions are restricted to either narrow ranges along Namibia's northern and southern borders or along a few dry river valleys (e.g., Kuiseb River) (Skinner and Smithers, 1990; Brain, 1988, 1990). The colobine molar is of interest in that colobines are generally rare throughout the late Miocene of Africa, the only other published specimens being a mandible from Ngeringerowa, an isolated molar from Nakali, possibly a premolar from Ngorora, all in Kenya, and the sample of "*Macaca flandri*" and *Libypithecus* from northern Africa (Benefit and Pickford, 1986; Pickford, 1987; Szalay and Delson, 1979). Colobines do not become common and diverse in the East African fossil record until the Pliocene. Similarly, if the Harasib deciduous molar can be attributed to a cercopithecine, then this is also of interest in that this group is also rare in the late Miocene of East Africa, the earliest confirmed presence in East Africa being younger than 5 Ma.

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